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Seasonal changes in phytoplankton composition and nutrient limitation in a shallow Baltic lagoon

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In this study we follow seasonal changes in the phytoplankton community composition in a shallow, mostly freshwater lagoon of the Baltic Sea. Nutrient enrichment effects on the quantitative and structural development of phytoplankton communities were also evaluated during short-term experiments in small-size enclosures. Different periods featuring alternate regulatory patterns of phytoplankton seasonal succession in the Curonian lagoon were derived. The spring phase is characterized by silica and phosphorus-limited conditions where nitrogen is a secondary limiting nutrient. Soluble inorganic phosphorus limits green algae, while silica limits diatoms, exclusively pennate species. In the enrichment experiments growth of centric diatom species was favoured by nitrogen addition, while pennates reaction was negative. Cyanobacteria dominated summer community is characterized by the nitrogen limitation, while phosphorus occurs as the secondary limiting factor. In general, inorganic nutrient concentrations in the hypereutrophic Curonian lagoon are too high to limit total plankton biomass, which is controlled mostly by the ambient physical factors. However, seasonal variation in nutrient concentrations could shape the phytoplankton community and, in combination with physical factors, force the seasonal succession.

Introduction

Seasonal changes in phytoplankton communities usually depend on seasonal variation of ambient physical factors and nutrient concentrations. Grazing on phytoplankton could provide another mechanism determining shifts in phytoplankton community. Mechanisms of seasonal succession are quite well studied both in fresh and marine waters (Levassseur *et al*. 1984, Sommer 1989, Gilabert 2001, Lau and Lane 2002, Gasiūnaitė *et al*. 2005). However, nutrient limitation patterns in marine ecosystems could be different due to the different sources and availability of limiting nutrients (Blomqvist *et al*. 2004). In estuarine systems more complex mechanisms are observed including co-limitation of nutrients (Aldridge *et al*. 1993, Malone *et al*. 1996, Maestrini *et al*. 1997). In temperate and boreal systems ambient physical factors are more important during the winter period; however, factors such as light and wind could also influence algae growth during the summer (Kanoshina *et al*. 2003, Pilkaitytė and Razinkovas 2006). There is also a clear evidence that salinity changes, even in a quite narrow range, could shape the phyto-

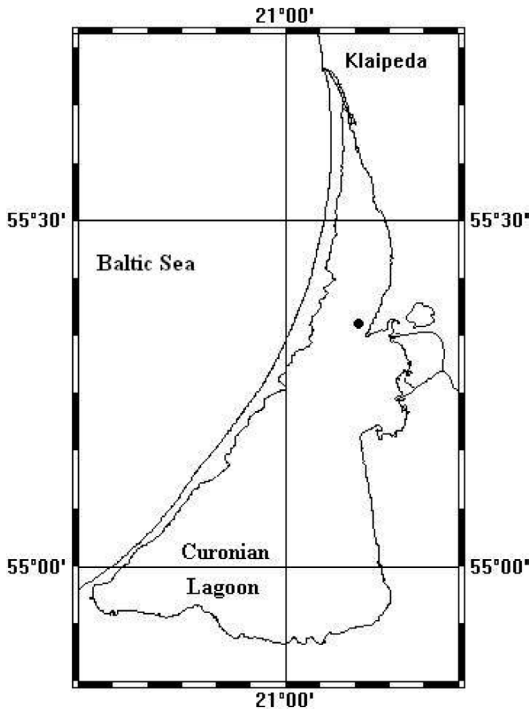

Fig. 1. Location of the study area. Dot indicates location of the experiment site.

plankton community in experimental conditions (Pilkaitytė *et al*. 2004) as well as along the geographical salinity range in the Baltic (Wasmund *et al*. 2000, Gasiūnaitė *et al*. 2005)

Seasonal succession of phytoplankton communities in eutrophic waters is directly related to seasonal "blooms". However, the mechanisms governing these phenomena could not be understood without knowing structural changes in phytoplankton community and specific relations between particular taxa and environmental conditions.

Recent experimental studies (Pilkaitytė and Razinkovas 2006) revealed the importance of different factors controlling chlorophyll *a* dynamics in the Curonian lagoon. However, the patterns and mechanisms of dominant phytoplankton taxa seasonal succession were not covered.

In this study we delineate chemical factors governing phytoplankton seasonal succession at different stages in the eutrophied estuarine lagoon. For that, nutrient enrichment effects on the quantitative and structural development of phytoplankton community were assessed.

Material and methods

Nutrient enrichment experiments (addition of phosphorus, nitrogen, and silicon) were carried out in the central part of the Curonian lagoon (Fig. 1), which is a temperate shallow eutrophic basin, connected to the southeastern Baltic Sea through the narrow Klaipėda strait. The southern and central parts of the lagoon contain fresh water due to discharge mainly from the Nemunas river.

In the experiments we used ten-litre transparent capped polyethylene enclosures. Due to small enclosure volume and to prevent the lack of nutrients or sedimentation, experiments were run for 48 hours, which is expected to be sufficient time for phytoplankton response (Bukaveckas and Shaw 1998). A batch of enclosures was placed in the upper water layer, 0.15 m below surface. Each nutrient enrichment experiment comprised 12 enclosures of four triplicate (Table 1). Nutrients were added in amounts sufficient to double the natural Curonian lagoon concentrations (Table 1). Due to the important role of large filamentous cyanobacteria in the Curonian lagoon, it was impossible to remove zooplankton from samples by filtering.

We measured chlorophyll *a* (Chl *a*) and nutrient (NO_3-N, PO_4-P, NH_4-N, SiO_2-Si) concentrations as well as phytoplankton community taxonomic composition at the start and at the end of each experiment. However, we analyzed taxonomically only integrated sample of replicates. Rough taxonomic phytoplankton species composition (except picoplankton species) and phytoplankton density were identified and counted using Utermöhl technique, as well as phytoplankton biomass was estimated from geometrical shapes. For further analyses samples taken at the beginning of experiments were classified according to the phytoplankton community structure, morphology and size into the two typical seasonal assemblages: spring and summer (Pilkaitytė, 2007). Phytoplankton growth rate for each taxonomic group was calculated as a difference between biomass at the end and at the start of each experiment. Differences between separate experiments, treatments, and phytoplankton species/higher taxa were tested with the *G*-test (contingency tables) after Williams's correc-

tion and compared with the χ^2-distribution with degrees of freedom according to Sokal and Rohlf (1997) and references therein.

Results

The dynamics of phytoplankton biomass and chlorophyll *a* followed two-maxima (spring and summer) succession pattern (Fig. 2). Diatoms were the most abundant group during the spring and in some cases, comprised the large part of biomass in the summer. Cyanobacteria usually dominated in August–September. However, in 2000 they were already abundant in early June. *Aphanizomenon flos-aquae*, *Anabaena* spp., and *Planktothrix agardhii* were the most numerous and dominant species. Of green algae, *Oocystis* spp., *Pediastrum* spp., and *Scenedesmus* spp. were the most numerous during the study period. However, total green algae biomass comprised only up to 20% of the total biomass. In a few cases, undefined flagellates ("other" group) were responsible for nearly half of the total phytoplankton biomass.

Nutrient concentrations generally decreased during all experiments both in the control and in enclosures enriched with the nutrients, except for the PO_4-P in the enclosure enriched with silica, and the NO_3-N in control and P-enriched enclosure during the summer. These changes, however, were small (Fig. 3).

Diatom species reacted to the nutrient enrichment according to their taxonomic division and morphology. Therefore, all pennate diatoms were analysed as one group and centric diatoms as another. The differences in centric and pennate diatoms growth rates during the spring between control and in enclosures enriched with N, P, and Si separately were statistically reliable (Table 2 and Fig. 4). The pennate diatoms growth rate was much higher in the enclosure with silica addition. Meanwhile the addition of nitrogen stimulated the growth rate of centric diatoms, while the growth rate of pennate diatoms in this treatment was even lower than that of the control (Fig. 4). The phosphorus addition stimulated growth of both diatom groups and the difference from the control was statistically significant ($p < 0.01$). Despite the growth rates of diatoms during

Table 1. Nutrient enrichment (Control = 0).

Date	P (µmol l^{-1})	N (µmol l^{-1})	PN (P + N, µmol l^{-1})	Si (µmol l^{-1})
29 Mar. 2000	4.5	114	4.5 + 114	–
12 Apr. 2000	4.5	114	4.5 + 114	–
26 Apr. 2000	4.5	114	4.5 + 114	–
15 May 2000	1.9	28.6	1.9 + 28.6	–
7 June 2000	1.9	28.6	1.9 + 28.6	–
24 July 2000	1.9	28.6	1.9 + 28.6	–
28 Aug. 2000	1.9	28.6	1.9 + 28.6	–
25 Apr. 2001	4.5	–	4.5 + 114	16.8
7 May 2001	4.5	114	4.5 + 114	–
21 May 2001	4.5	114	4.5 + 114	–
4 June 2001	1.9	28.6	1.9 + 28.6	–
27 June 2001	1.9	28.6	1.9 + 28.6	–
17 July 2001	1.9	28.6	1.9 + 28.6	–
20 Aug. 2001	1.9	28.6	1.9 + 28.6	–
1 Oct. 2001	1.9	28.6	1.9 + 28.6	–
10 Apr. 2002	4.5	–	4.5 + 114	16.8
22 Apr. 2002	4.5	–	4.5 + 114	16.8
6 May 2002	4.5	–	4.5 + 114	16.8
20 May 2002	1.9	–	1.9 + 28.6	6.6
4 June 2002	1.9	–	1.9 + 28.6	6.6
17 June 2002	1.9	28.6	1.9 + 28.6	–
9 Sep. 2002	1.9	28.6	1.9 + 28.6	–
23 Sep. 2002	1.9	28.6	1.9 + 28.6	–

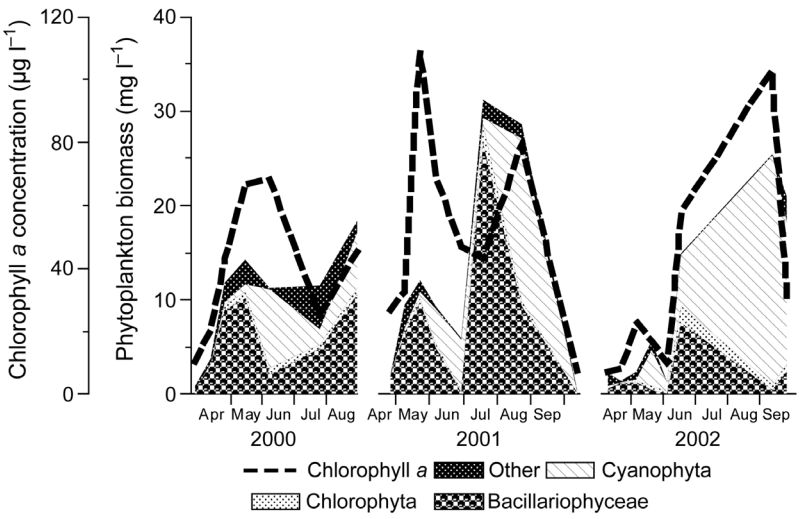

Fig. 2. Seasonal development of main phytoplankton groups and chlorophyll *a* during the study period.

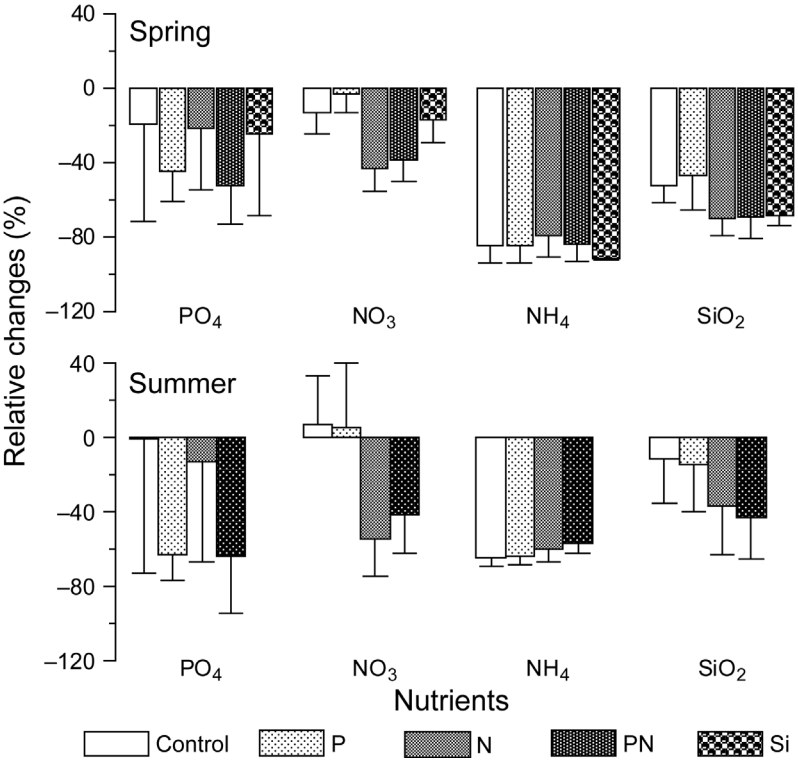

Fig. 3. Relative nutrient concentration changes (%, + 0.5 SD) during experiments.

the summer were low, the difference between the P enrichment and control was significant at ($p < 0.05$).

The growth rate of cyanobacteria during the spring was quite low. During the summer the growth rates of dominant species: *A. flos-aquae*, *Anabaena* spp., and *P. agardhii* in the enclosures enriched with both N and P significantly differed from that of the control, while separate additions of these two nutrients did not produce any statistically significant effect (Table 2 and Fig. 5). Nevertheless, addition of phosphorus induced higher growth rate of the nitrogen fixing *Anabaena* species. Other cyanobacteria species did

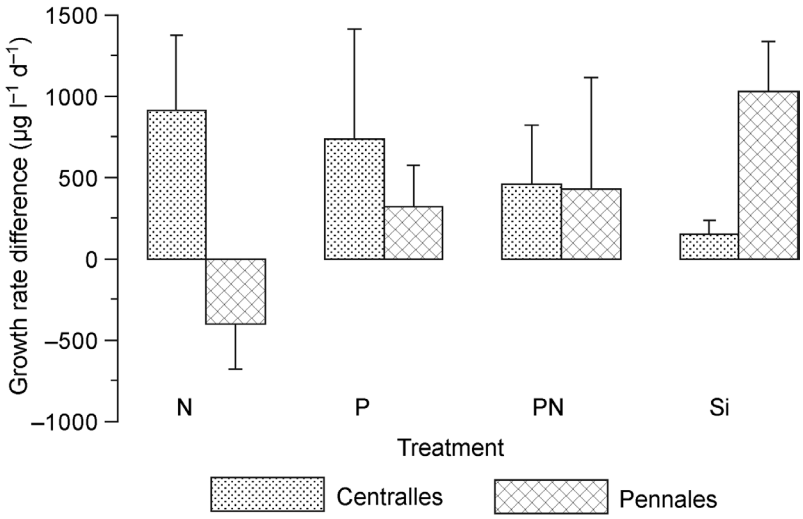

Fig. 4. The pennate and centric diatoms growth rate difference (+ 0.5 SD) between treatments and the control during the spring. Treatment: N = enriched with nitrogen, P = enriched with phosphorus, PN = enriched with both nitrogen and phosphorus, Si = enriched with silica.

not show statistical variation in growth rates as as compared with that of the control.

All the Chlorococcales species reacted to the nutrient enrichment in a similar way. Therefore, only the dominant species were analysed. Differences in growth rates of these species when enriched with both P and N and the control were statistically significant in the spring ($p < 0.05$) and summer ($p < 0.001$). Addition of phosphorus induced statistically significant ($p < 0.05$) growth-rate increase during the spring, while nitrogen addition stimulated the growth during the summer ($p < 0.01$) (Table 2).

Discussion

Factors influencing phytoplankton development during the spring

The highest nutrient concentrations in the Curonian lagoon are observed in early spring: about 114.3 μmol l^{-1} NO_3-N, 6.1 μmol l^{-1} PO_4-P, and 180 μmol l^{-1} SiO_2-Si. Generally, the early spring phytoplankton biomass could be regarded as limited only by ambient physical conditions (Pilkaitytė and Razinkovas 2006). Diatoms are well adapted to stronger mixing and lower light irradiance (Lindenschmidt and Chorus 1998, Litchman 1998, Flöder *et al*. 2002). This could be the reason for these algae to thrive (Fig. 2) when the lagoon is active hydraulically (Gasiūnaitė and Razinkovas 2004).

Further limitation patterns, however, could be different. Sharp silica depletion in April to around 2.5 μmol l^{-1} SiO_2-Si (Pilkaitytė and Razinkovas 2006) points towards a possible silica limitation-forced diatom succession, as occurs in many other waterbodies during the spring (Conley 1999). At that time, the pennate diatom growth rate increase in Si enriched enclosures, while the centric species growth rate remains low (Fig. 4). Though, it could be suggested that silicon limits not all diatoms, but rather pennate group, while the centric diatoms were not limited.

On the other hand, nitrogen is also important for siliceous algae development as diatoms are

Table 2. The heterogeneity *G* values of phytoplankton growth rate as compared with that of the control. Significant differences indicated as follows: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

		Bacillariophyceae	Chlorophyta	Cyanobacteria
	df	1	2	2
Spring				
	P	10.9**	8.7*	0.1
	N	69.3***	0.1	0.2
	PN	0.4	6.5*	0.1
	Si	22.2***	5.1	0.4
Summer				
	P	5.9*	2.2	2.5
	N	2.0	10.3**	8.0*
	PN	0.9	18.5***	52.2***

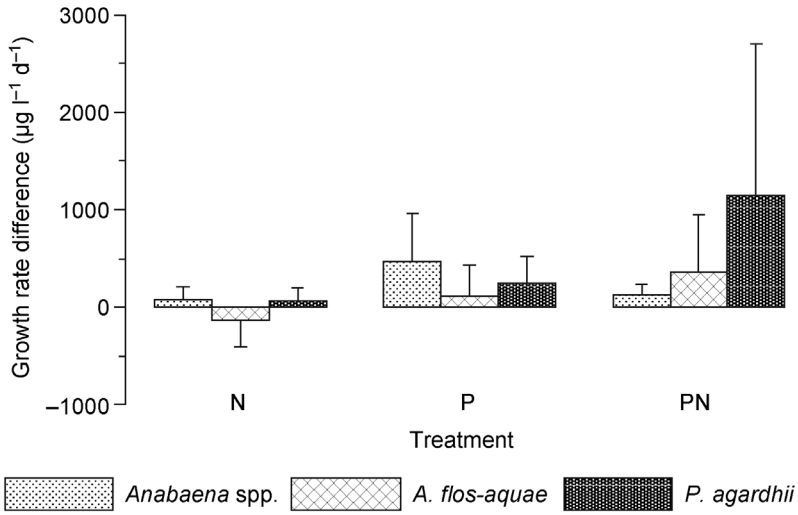

Fig. 5. The dominant cyanobacteria species growth rate difference (+ 0.5 SD) between treatments and the control during the summer. Treatment: N = enriched with nitrogen, P = enriched with phosphorus, PN = enriched with both nitrogen and phosphorus.

known as inferior competitors for that type of resource (Interlandi *et al*. 1999). In the nutrient enrichment experiments, nitrogen addition enhanced the centric diatoms growth rate, while pennate species growth rate decreased (Fig. 4). The phosphorus also induced higher growth rate in centric diatoms.

Later, in May, along with the reduction in Nemunas river discharges the lagoon hydraulically shifts from the lentic to limnic state (Gasiūnaitė and Razinkovas 2004) which is less beneficial for diatoms, which favour turbulent conditions.

Phosphorus is another nutrient influencing the phytoplankton community development throughout the spring. The N:P ratio is quite high from March to May (Fig. 6), suggesting phosphorus deficiency. Phosphate concentrations close to the limitation threshold observed at that time also confirm the evidence of a P limitation period in spring as is suggested for other estuarine systems (Malone *et al*. 1996, Maestrini *et al*. 1997). Both centric and pennate diatoms and green algae reacted positively to the P enrichment. Additionally, as compared with that of the control, growth rate of green algae increased significantly ($p < 0.05$) as a result of PN enrichment. It is known that green algae are more sensitive to nitrogen deficiency, but could be also limited by low phosphorus concentration (Sommer 1989). Phosphorus is the first nutrient to deplete in spring and nitrogen depletes later on. These results indicate that phosphorus is the primary limiting nutrient during the spring, while the nitrogen availability is sufficiently low to become secondary limiting nutrient.

Factors influencing phytoplankton development during summer

Phosphate concentration starts to grow in the early summer while nitrate concentration is still low (8 μmol l^{-1} NO_3-N). At this stage phytoplankton community in the Curonian lagoon as a whole is known to be nitrogen limited (Pilkaitytė and Razinkovas 2006).

The nitrogen could limit green algae, or at least some species: *Dictyosphaerium* spp., *Scenedesmus* spp., *Monoraphidium* spp. (Sommer 1989, Makulla and Sommer 1993), which in the Curonian lagoon could be even dominant during the summer (Olenina 1998). This is also supported by the nutrient enrichment experiment data as N addition was statistically significant for the green algae growth (Table 2). However, the growth rate of green algae enriched with PN was higher as compared with that of the control, suggesting that phosphorus could be a secondary limiting nutrient.

The cyanobacteria biomass increases rapidly when the water temperature reaches 20 °C, usually at the end of June–beginning of July, and remains high until the end of October–beginning

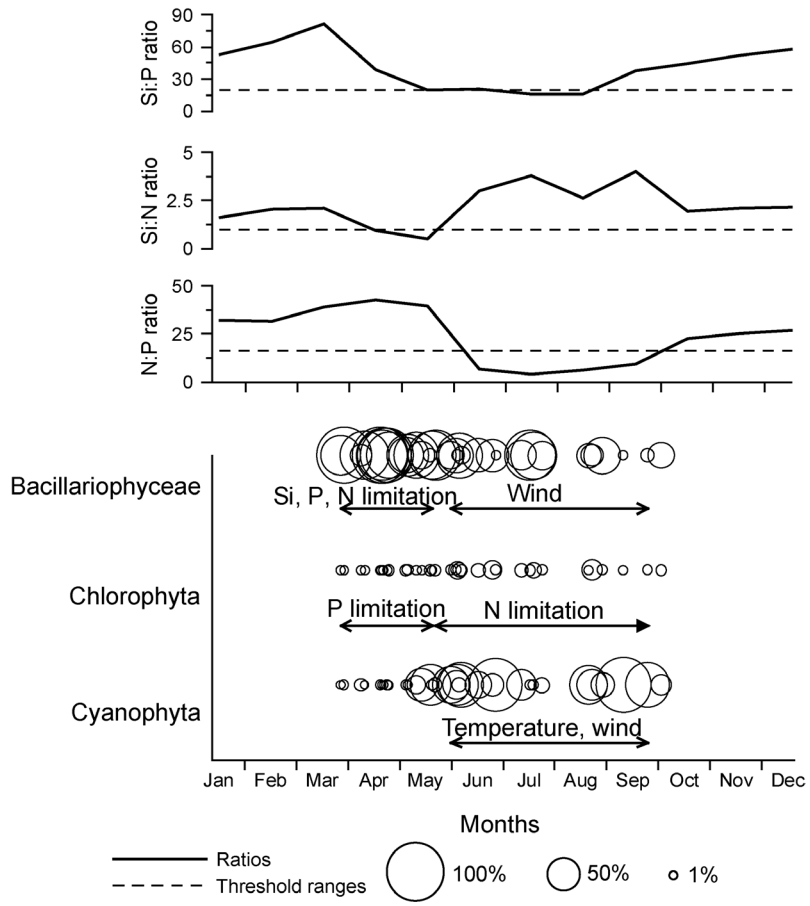

Fig. 6. Generalised scheme of phytoplankton seasonal succession mechanisms in the Curonian lagoon. Upper panel: nutrient ratio averages (unpubl. state monitoring data 1984–2000) along with threshold ranges (Sommer 1999 and references therein). Lower panel: Phytoplankton group dynamics (bubbles correspond to the percentage of the total biomass).

of November (Olenina and Olenin 2002), which is in good agreement with the present study (Fig. 2). High temperature (Kanoshina *et al*. 2003) and high irradiance (Havens *et al*. 2003) both favour nitrogen-fixing cyanobacteria (including *A. flos-aquae* and *Anabaena* spp.) development during the summer. Generally, the results of the nutrient enrichment experiments point out that both N and P additions significantly increased cyanobacteria growth rates as compared with those of the control (Table 2). The significant difference in the growth rate in the N-enriched enclosures as compared with that of the control could be due to the decline of the nitrogen fixing *A. flos-aquae* (Fig. 5). Similar results regarding *A. flos-aquae* reaction to P enrichment were published for the Archipelago Sea (Lagus *et al*. 2002).

The abundant herbivorous zooplankton, mainly *Chydorus sphaericus* and *Daphnia* spp., in the Curonian lagoon during the summer could graze out the smaller algae and therefore give additional advantage to large cyanobacteria (Razinkovas and Gasiūnaitė 1999). In addition, due to toxicity and/or aggregates formation, the bloom forming cyanobacteria are more resistant to grazing (Sommer *et al*. 1986, Sommer *et al*. 2001). In that case, zooplankton is not able to control the whole phytoplankton community dynamics during the cyanobacteria bloom in the Curonian lagoon as it does in eutrophied freshwater waterbodies (Sommer *et al*. 1986).

During the summer, diatom growth is supposedly restricted by the lower irradiance (Tilman *et al*. 1986, Litchman 1998, Flöder *et al*. 2002), which is diminished by phytoplankton attenuation and low turbulence, as they require well-mixed conditions (Lindenschmidt and Chorus 1998). Stronger wind could mix water masses and could blow and/or disturb formed cyanobacteria blooming aggregates. Under such conditions diatoms could become dominant again in the phytoplankton community replacing cyano-

bacteria. The high diatom abundance events during the summer could be an example of this situation, as is seen in Fig. 2.

Our experiments demonstrated that despite the high absolute inorganic nutrient concentrations in the hypereutrophic Curonian lagoon, seasonal changes in relative nutrient availability could shape the phytoplankton community at the species and higher taxonomic group levels. In combination with abiotic factors different periods featuring alternate regulatory patterns of phytoplankton seasonal succession in the Curonian lagoon can be derived (Fig. 4). The first phase, restricted to winter and early spring, is characterized by nutrient-unlimited phytoplankton growth controlled only by ambient physical conditions. The second — spring phase — is characterized by silica and phosphorus-limited conditions where nitrogen is a secondary limiting nutrient. Soluble inorganic phosphorus limits green algae, while silica limits diatoms, exclusively pennate species. The growth of centric diatom species was favoured by nitrogen addition. The shift from spring diatom-dominated community in May could also be supported by decrease in turbulence caused by both riverine discharge reduction and wind climate changes. The third phase is the nitrogen-limitation and presumable light-limitation (R. Pilkaitytė unpubl. data) period characterized by the domination of cyanobacteria and the highest phytoplankton biomass. Before the start of the third phase, a short intermediate "clear water" period featuring low phytoplankton abundance could be detected. During the summer, the Curonian lagoon phytoplankton community could be dominated either by the cyanobacteria or by the diatoms and the domination pattern is known to be decided by the temperature and wind (Pilkaitytė and Razinkovas 2006).

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